Capturing Evolution and Ecology in a Global Ocean Model

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Outline

- Challenges
  - Motivating scientific questions
- Approach
  - Existing models and their limitations
  - EVolutionary Ecosystem (EVE) model
- Results
  - Emergent phytoplankton growth strategies
  - Cell size, N:P composition, dynamic storage

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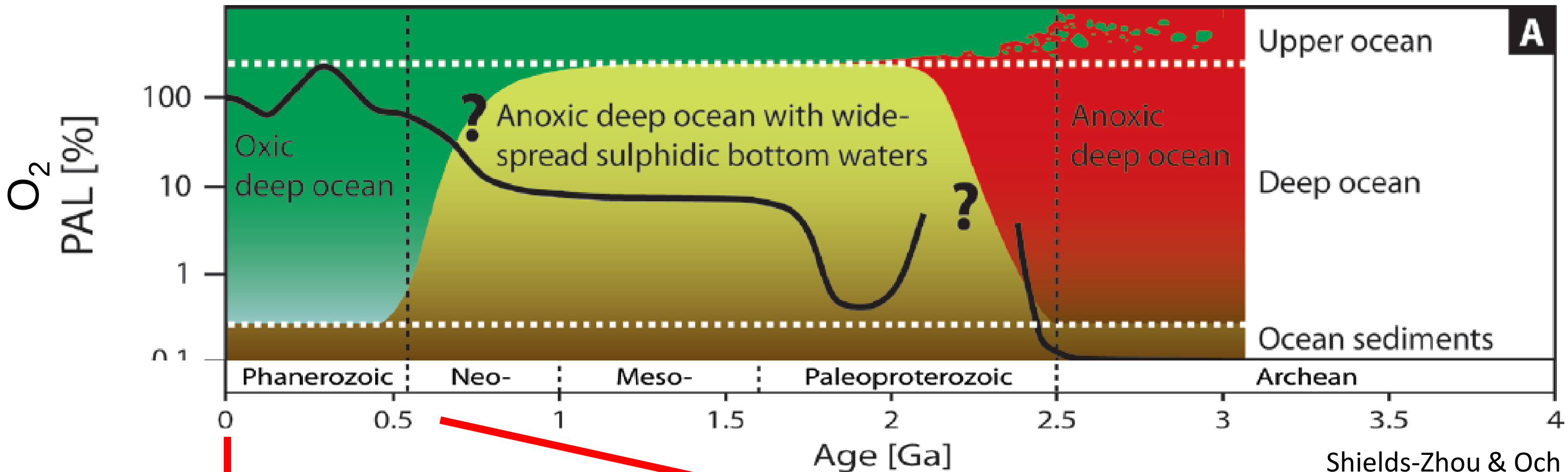
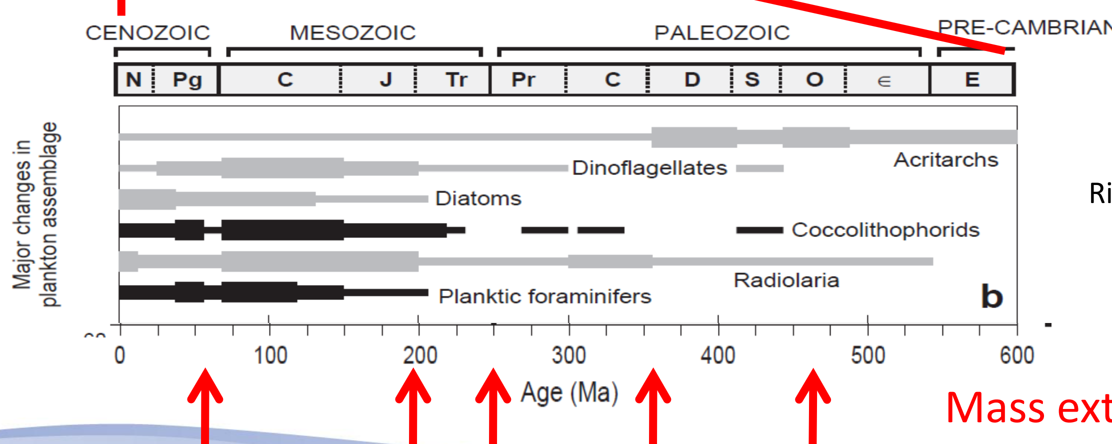
How have Earth and life co-evolved in the past?



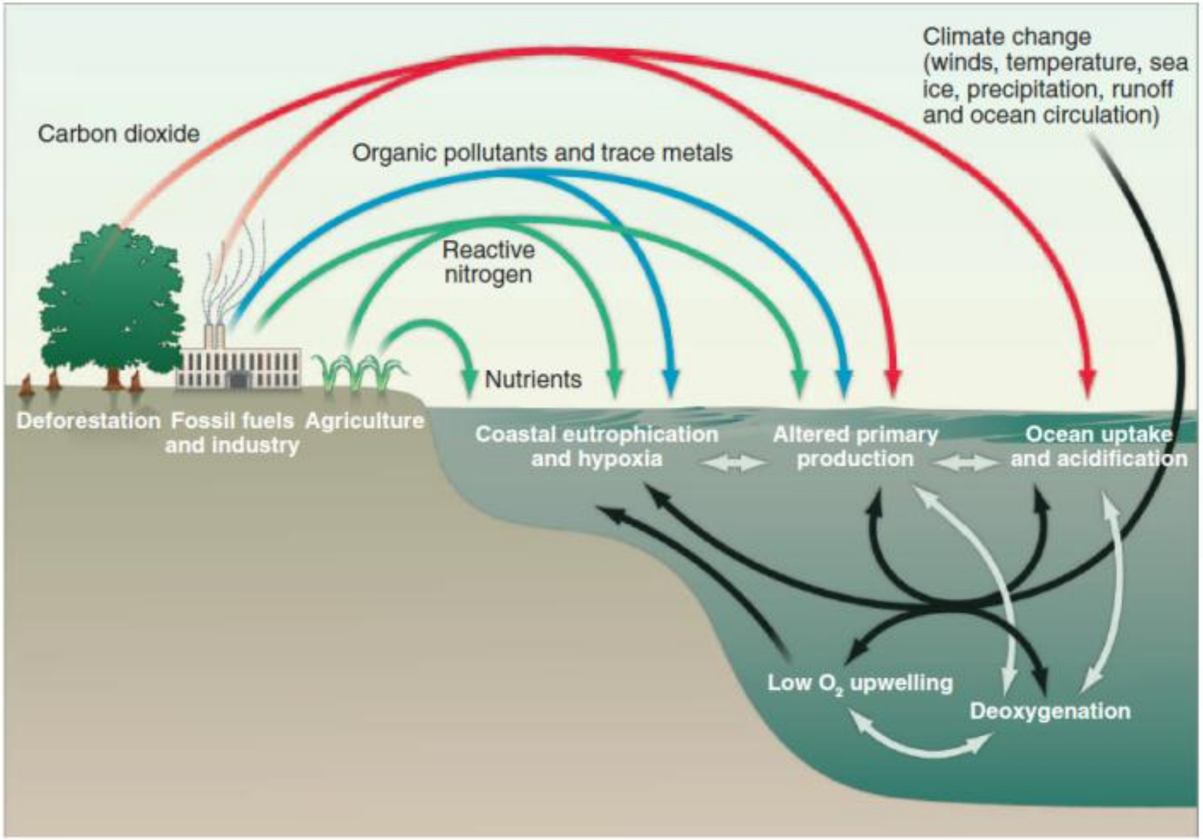
Shields-Zhou & Och (2011)



Ridgwell & Zeebe (2011)

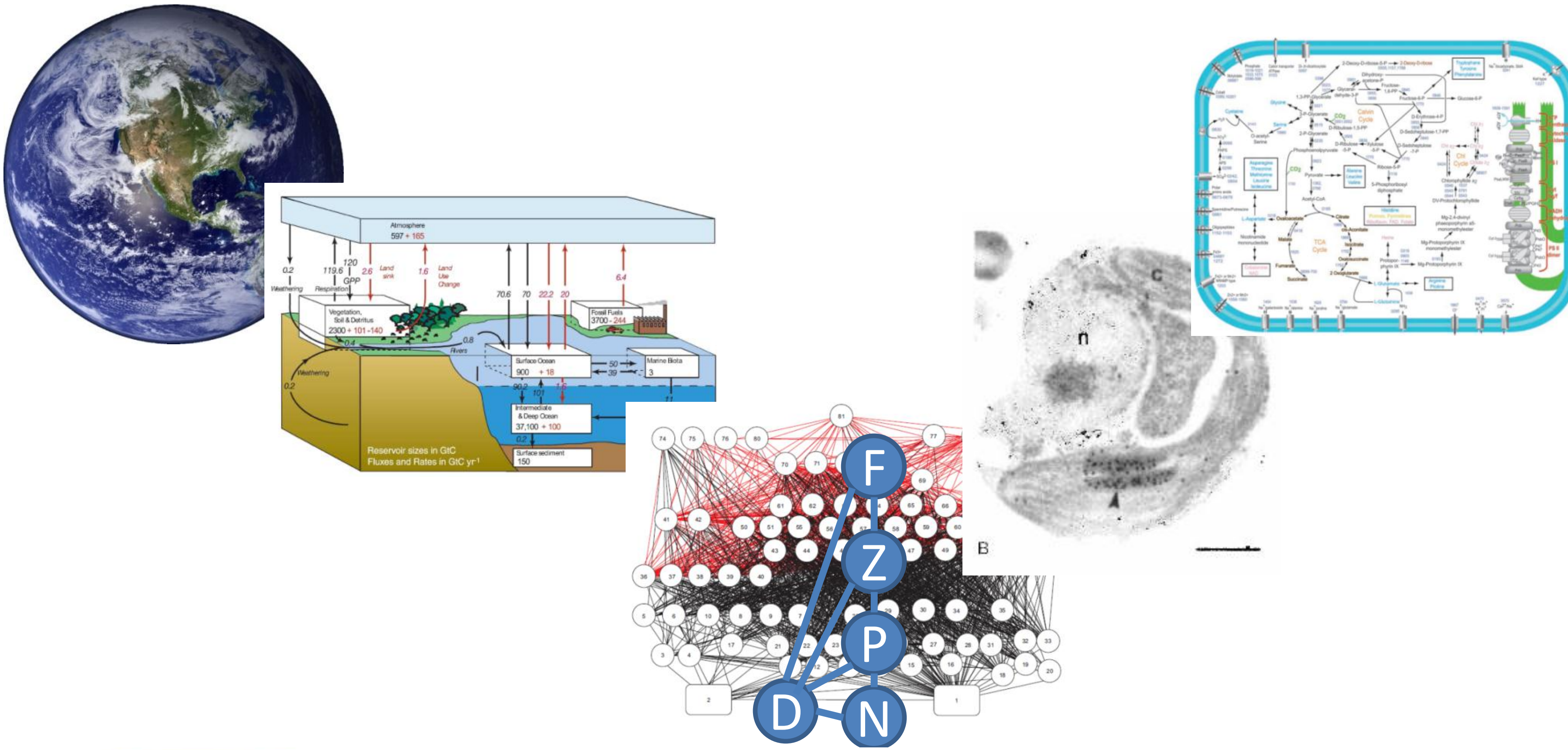
Mass extinctions

How will the (rest of the) biosphere respond to anthropogenic global change?



Doney (2010) *Science* 328: 1512-1516

How can we use (molecular) biological data to produce better predictive biosphere models?



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Overarching challenges

- Life is (very) diverse
- Life adapts
  - Organisms acclimate
  - Populations evolve by natural selection
- Organisms have life histories
- Evolution is contingent

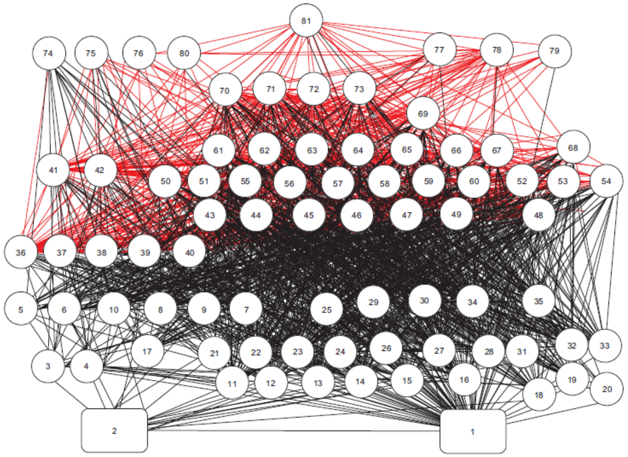
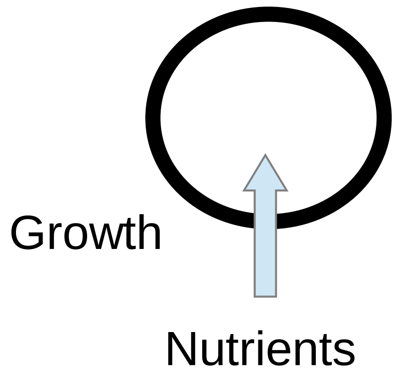
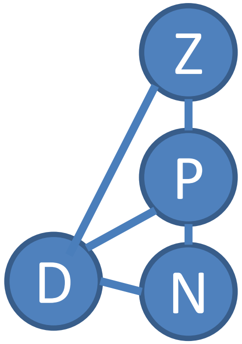


figure Mike St John, Link (2002)

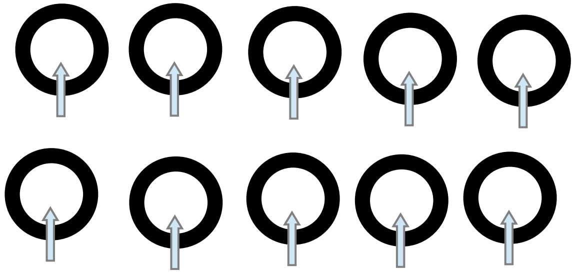
Traditional approaches to modelling the marine ecosystem



Monod (1942)



Riley (1946)



Plankton Functional Types

LeQuere et al (2000s)

Aggregated models - effective locally when tuned to observations in a region of space and time ...but not portable

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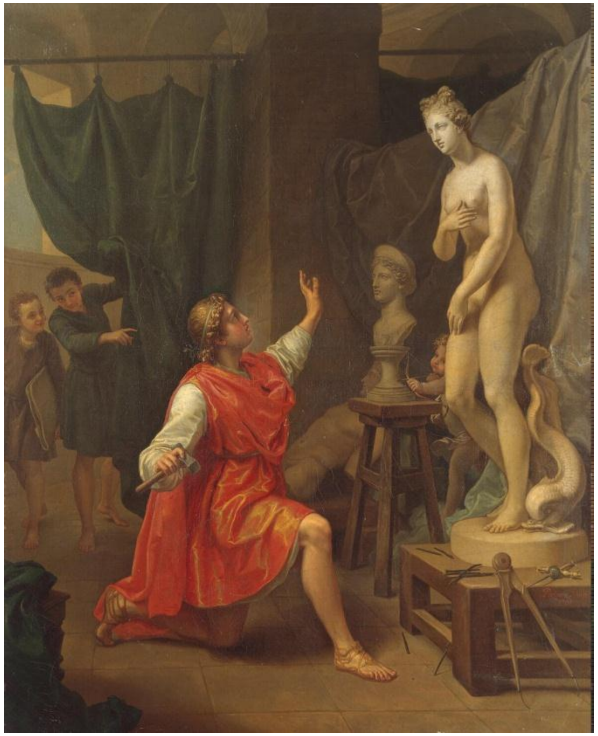
Limitations of traditional models

- Lack of diversity
- Fixed responses
  - No acclimation or adaptation
- Lack of life histories
  - Important for storage and acclimation strategies in dynamic environments, seasonality, dispersal
- Lack of evolutionary contingency
  - Can access anywhere in trait space



Pygmalion and Galatea
by Pecheux (1784)

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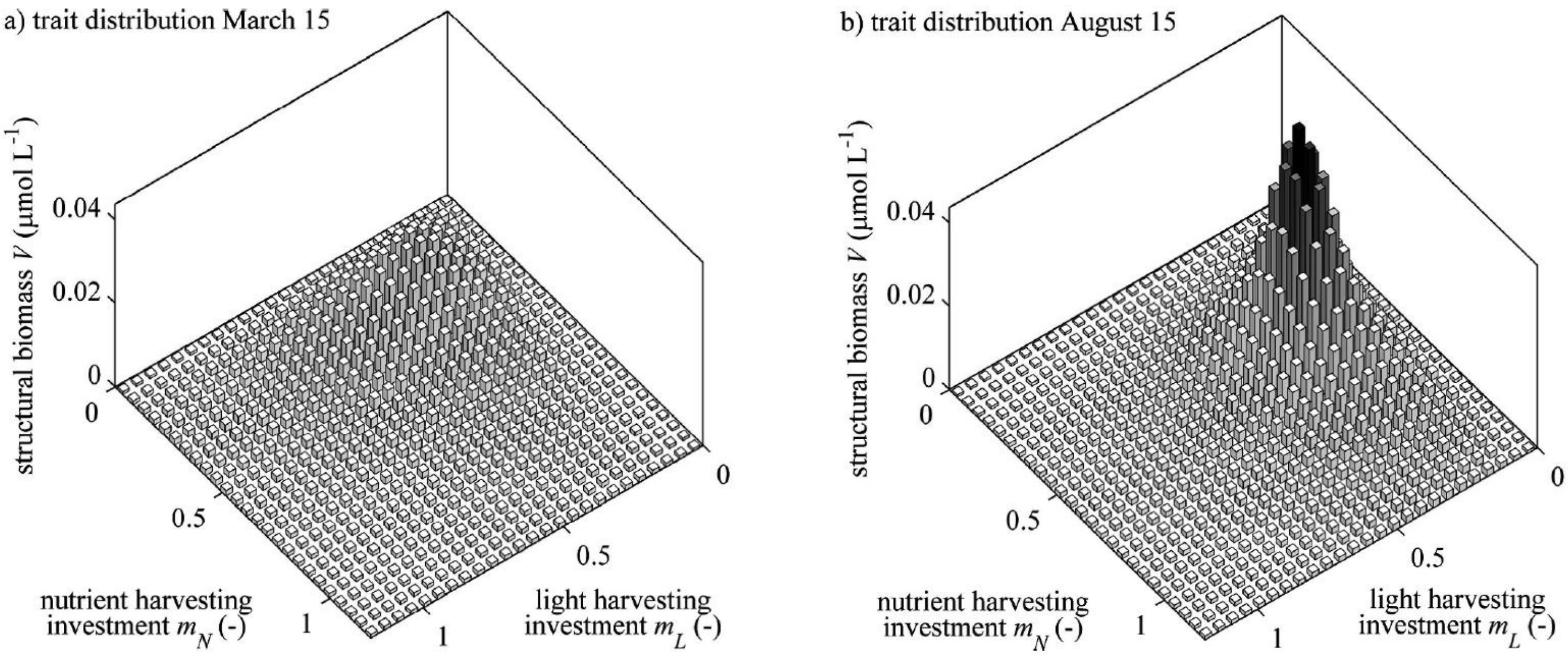
“A biodiversity-inspired approach to aquatic ecosystem modelling”



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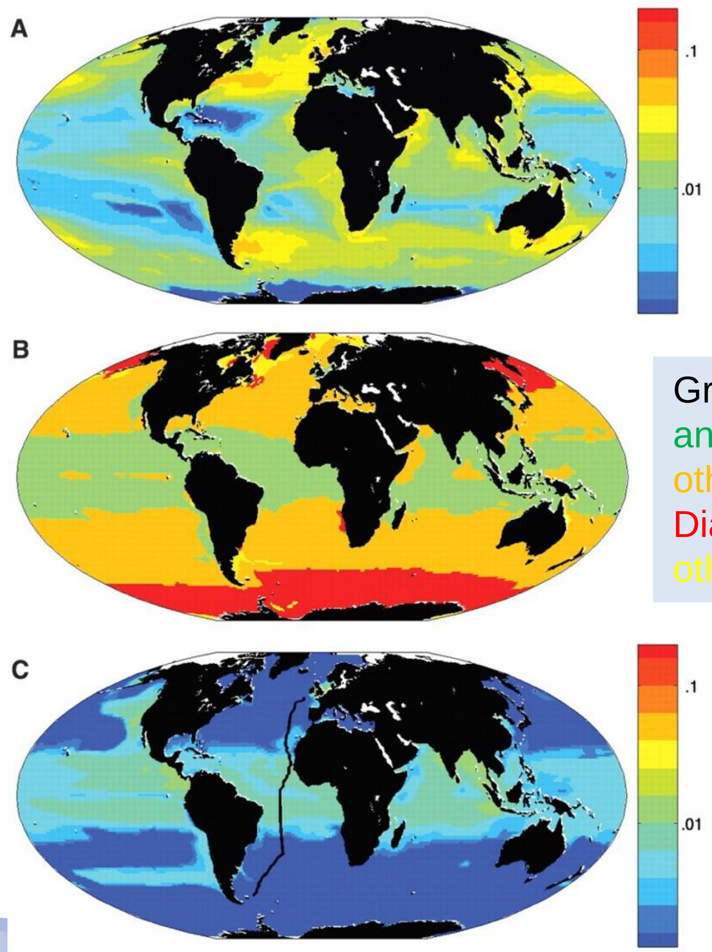
Bruggeman & Kooijman (2007) *Limnol. Oceanog.* 52: 1533-1544

“Emergent biogeography of microbial communities in a model ocean”



Total phytoplankton biomass
(μM P, 0 to 50 m average)

Group locally dominating annual mean biomass:
analogs of *Prochlorococcus*
other small photo-autotrophs
Diatoms
other large phytoplankton

Total biomass of
Prochlorococcus analogs
(μM P, 0 to 50 m average)

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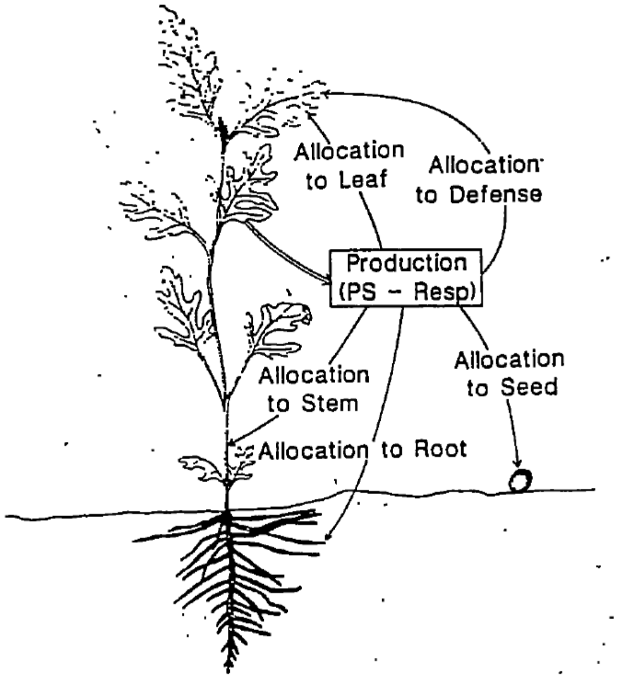
Follows *et al.* (2007) *Science* 315: 1843-1846

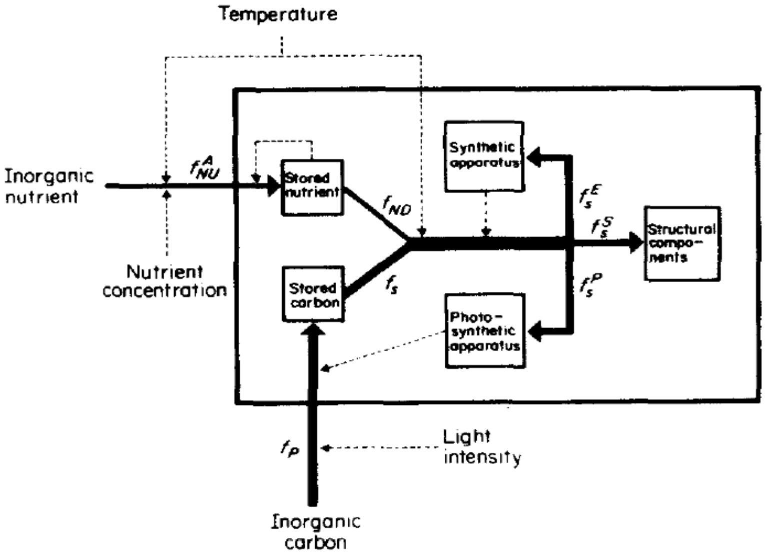
Evolutionary ecology:
Traits, trade-offs, emergent strategies

Terrestrial plants



Bloom (1985), Tilman (1990)

Phytoplankton



Shuter (1979), Raven (1984), Vallino *et al.* (1996)

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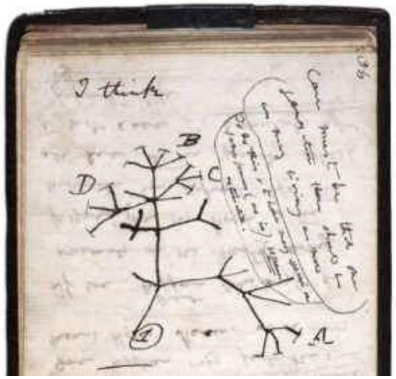
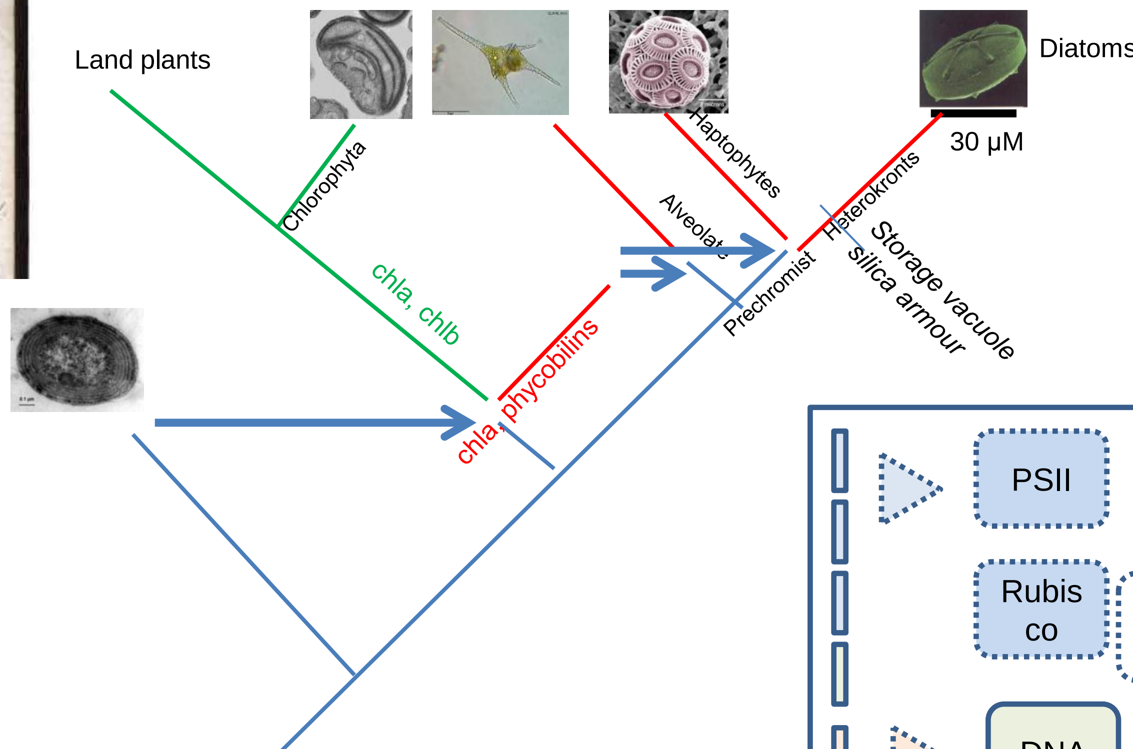
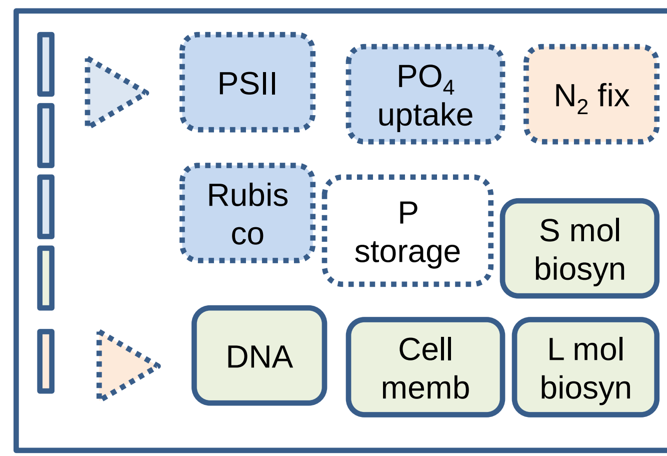
EVolutionary Ecosystem (EVE) Model Approach

- Individuals:
  - Functional traits
  - Physiologically constrained model organisms
  - Trade-offs and resource allocation
- Community and ecosystem:
  - Selection in model environment
  - Interactions and trophic structure
  - Community assembly (dispersal...)
  - Biogeochemical cycles

Conserved, phylogenetically-related building blocks







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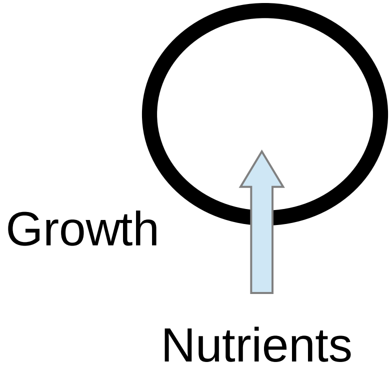
Falkowski *et al.* (2004) *Science* 305: 354-360

Physiology, 'cellular economics'

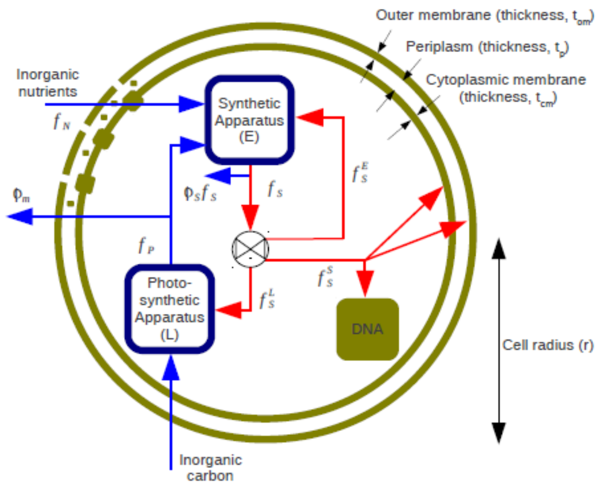
COMPLEXITY

Monod-type models



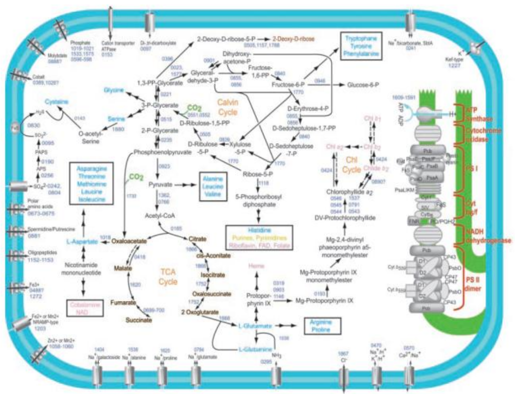
Monod (1942)

EVE model



Inspired by Shuter (1979)

Metabolic networks (systems biology)



Dufresne (2003)

⇨Parameter-sparse representation of diversity and adaptation based on common physiology

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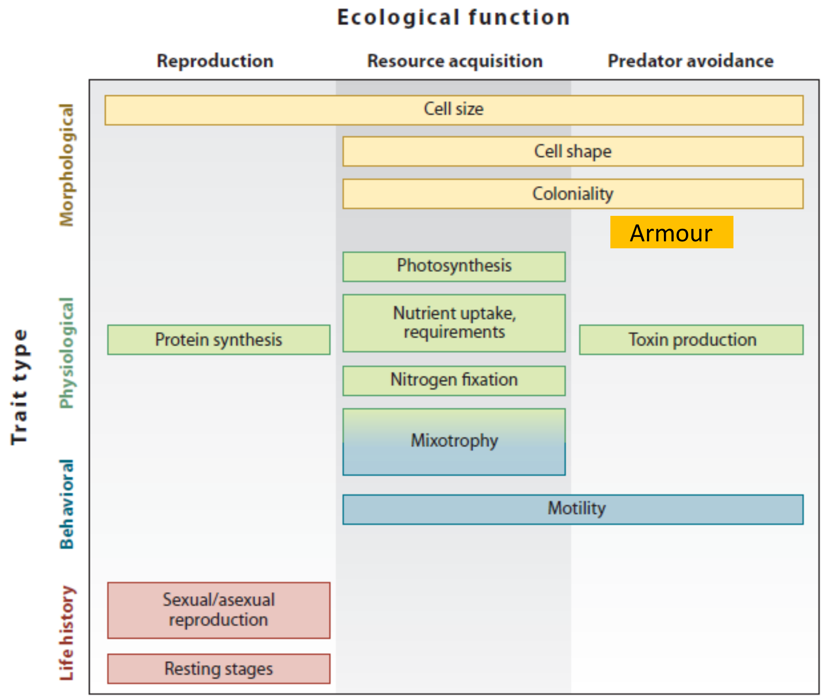
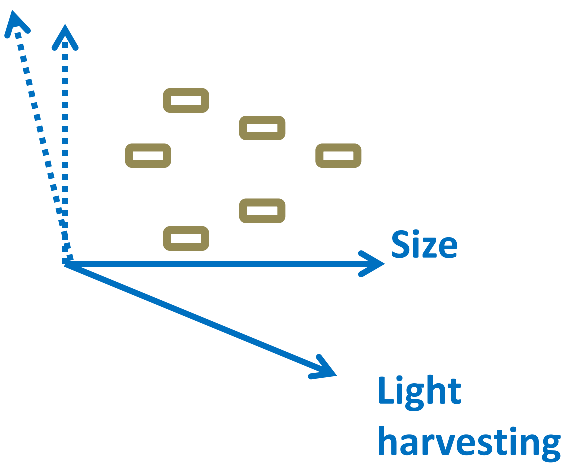
Functional traits and trade-offs

Phytoplankton traits



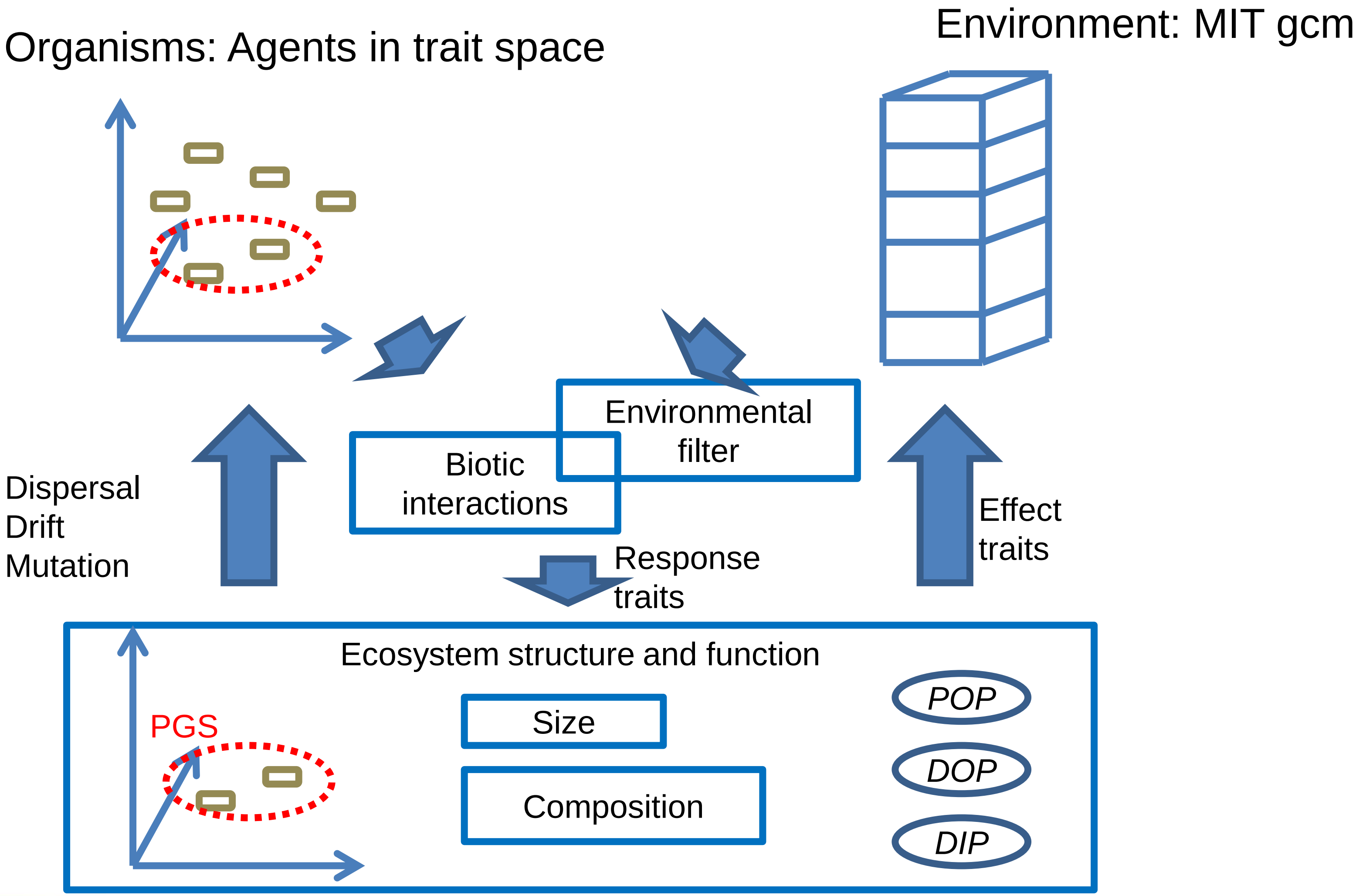
Trait space



Trade-offs emerge from physiological constraints and cost-benefit

Litchman, E., and C.A. Klausmeier. 2008. Annual Review of Ecology, Evolution, and Systematics 39: 615-639

Environmental selection



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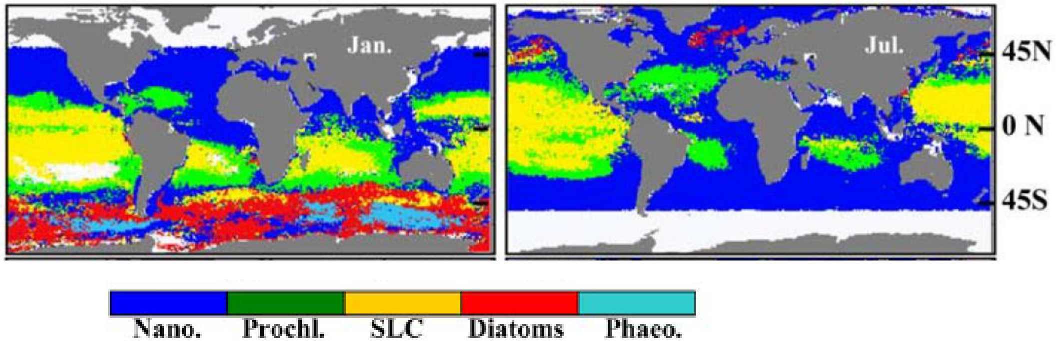
Applications

- Emergent phytoplankton growth strategies and biogeography

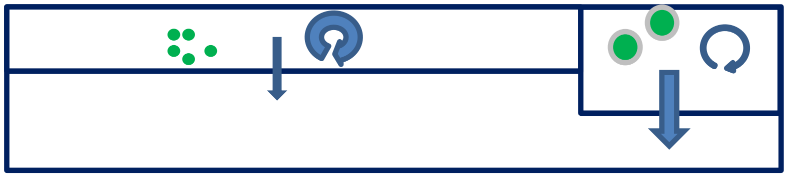
1. Cell (minimum) size
2. Composition and N:P stoichiometry
3. Dynamic strategies

1. Patterns in phytoplankton size

Biogeography (Alvain 2008)



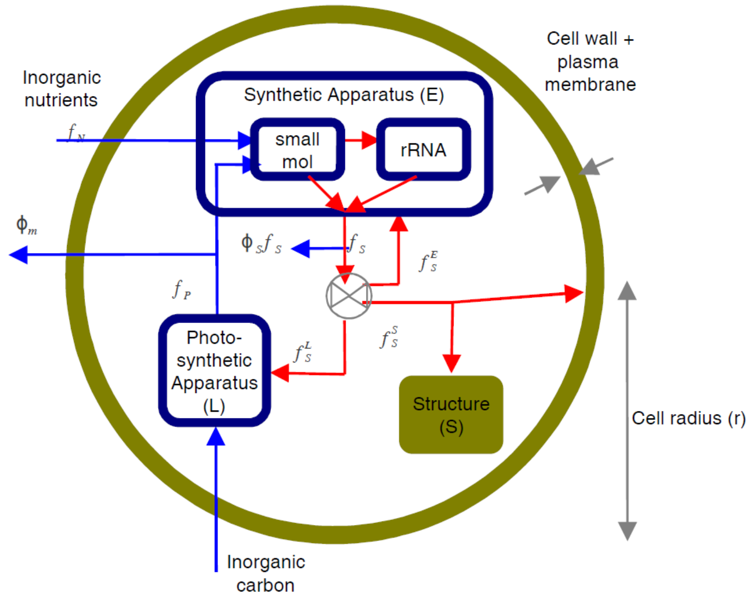
Pico < 2 µm
Nano 2 - 20 µm
Micro 20 – 200 µm

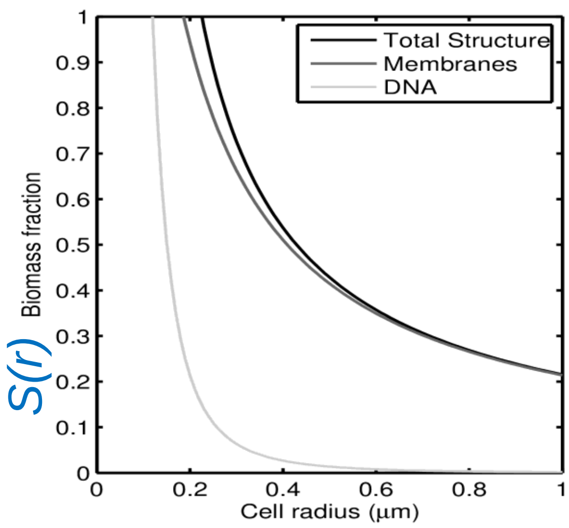


Oligotrophs / gleaners
‘K strategists’
Nutrient limited
< 1µm prokaryotes
95% efficient microbial loop
R*, small size

Copiotrophs / opportunists
‘r strategists’
Light-limited
>10 µm eukaryotes
Growth rate
Storage strategies

Model and minimum size constraint





Fogg (1991), Raven (1994,1999)

2D Trait space S(r)+E+L=1

Photosynthesis max rate $f_P = \kappa_P\, I\, L_{res}$

Biosynthesis max rate $f_S = \kappa_S\, E_{res}\, Q_{10}^{(T-T0)/10}$

Nutrient uptake max rate $f_N = \kappa_N\, c_\infty / r^2$

⇨ Growth rate $\mu = \min(f_P, f_S, f_N)$ -maintenance

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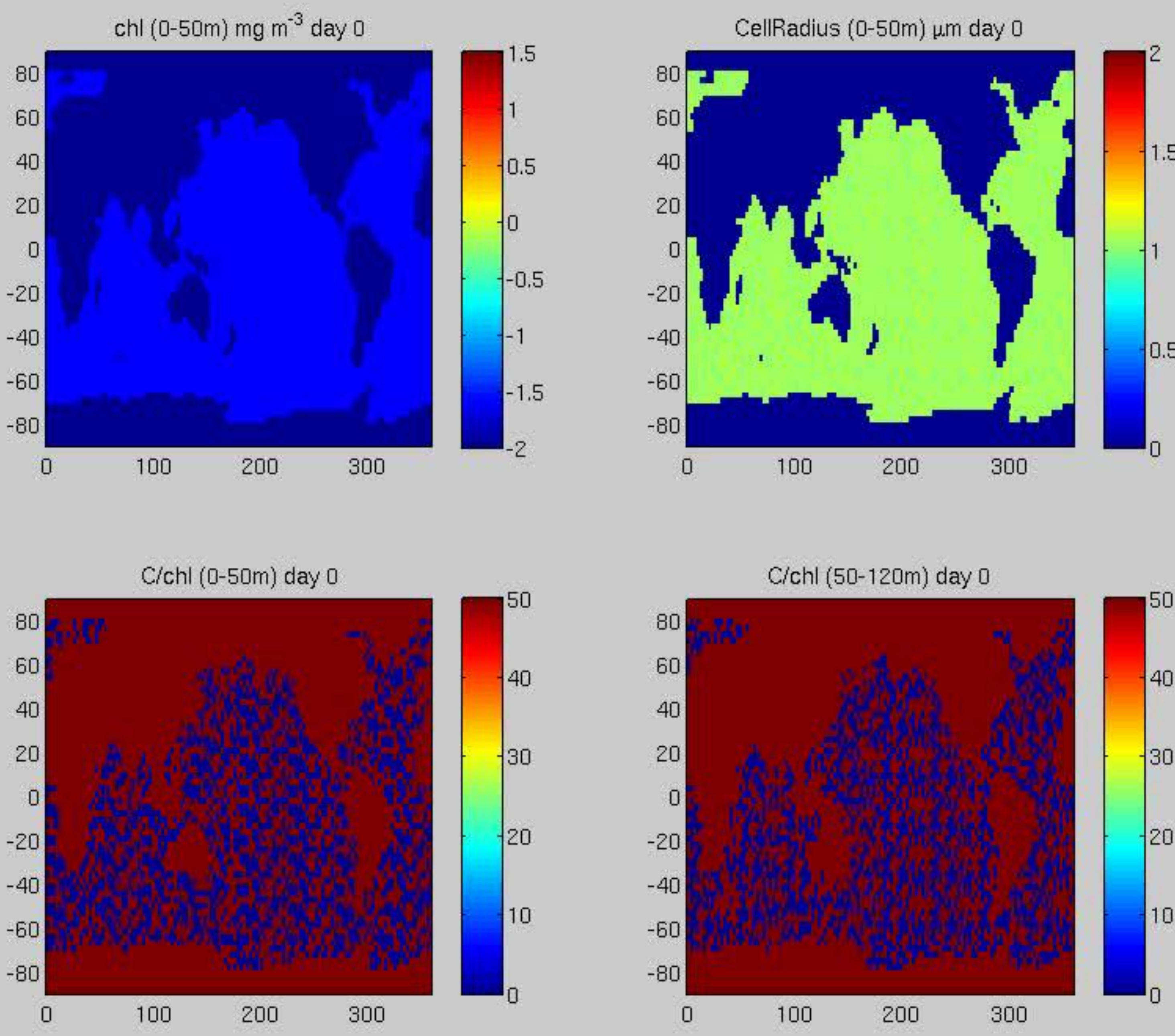
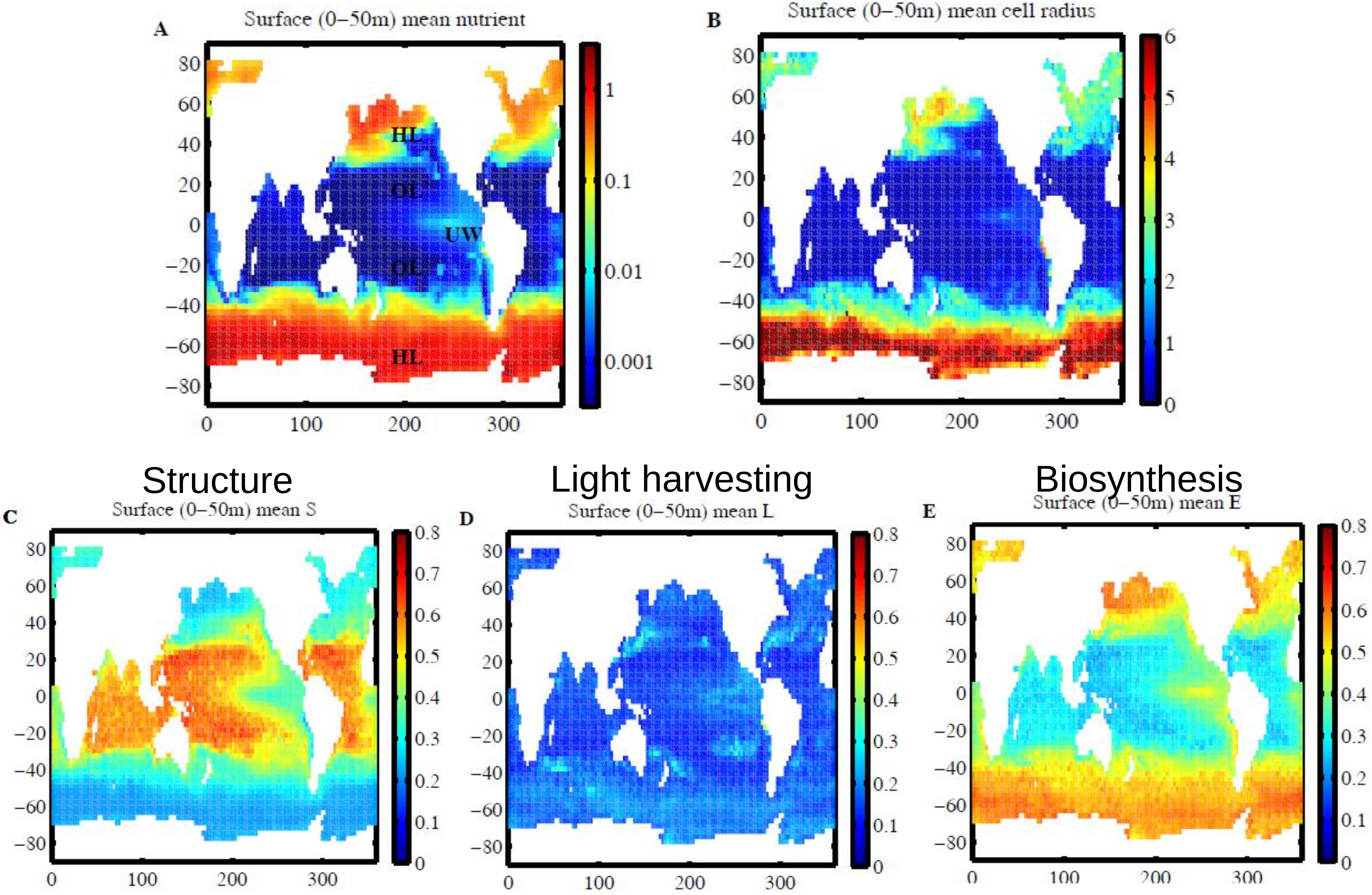
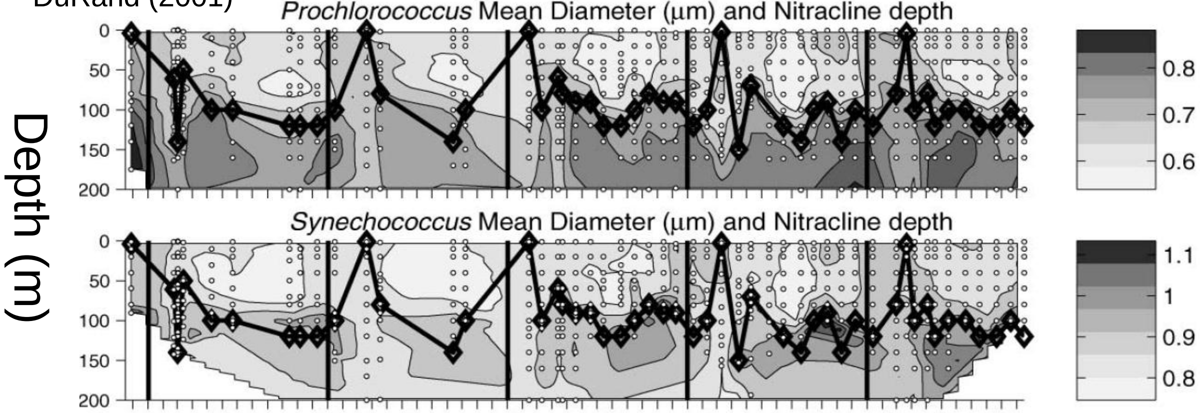

chl (0-50m) mg m-3 day 0
CellRadius (0-50m) µm day 0
C/chl (0-50m) day 0
C/chl (50-120m) day 0



Clark, Lenton, Williams, Daines (2013) *Limnol. Oceanog.* 58: 1008-1022

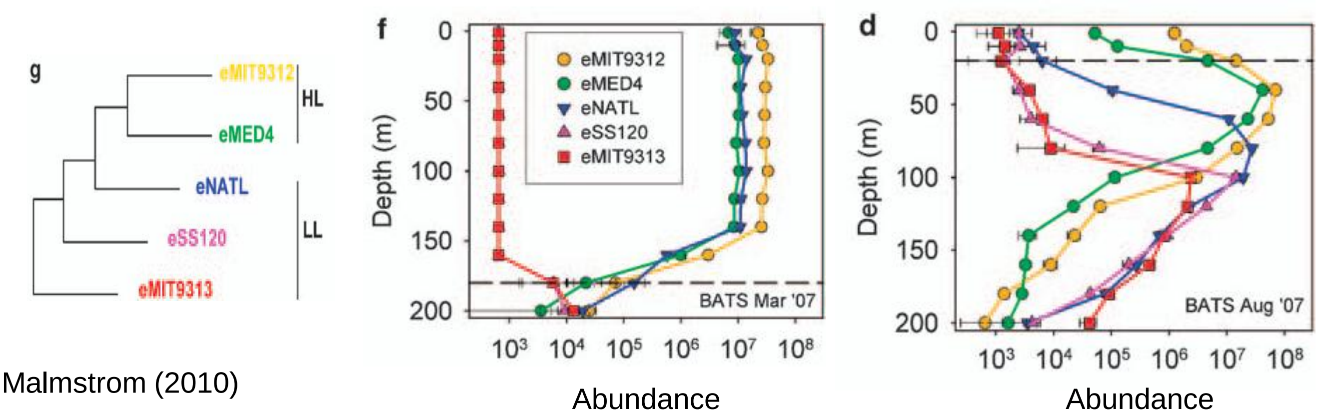
Cell size and adaptation to low light (BATS)

DuRand (2001)



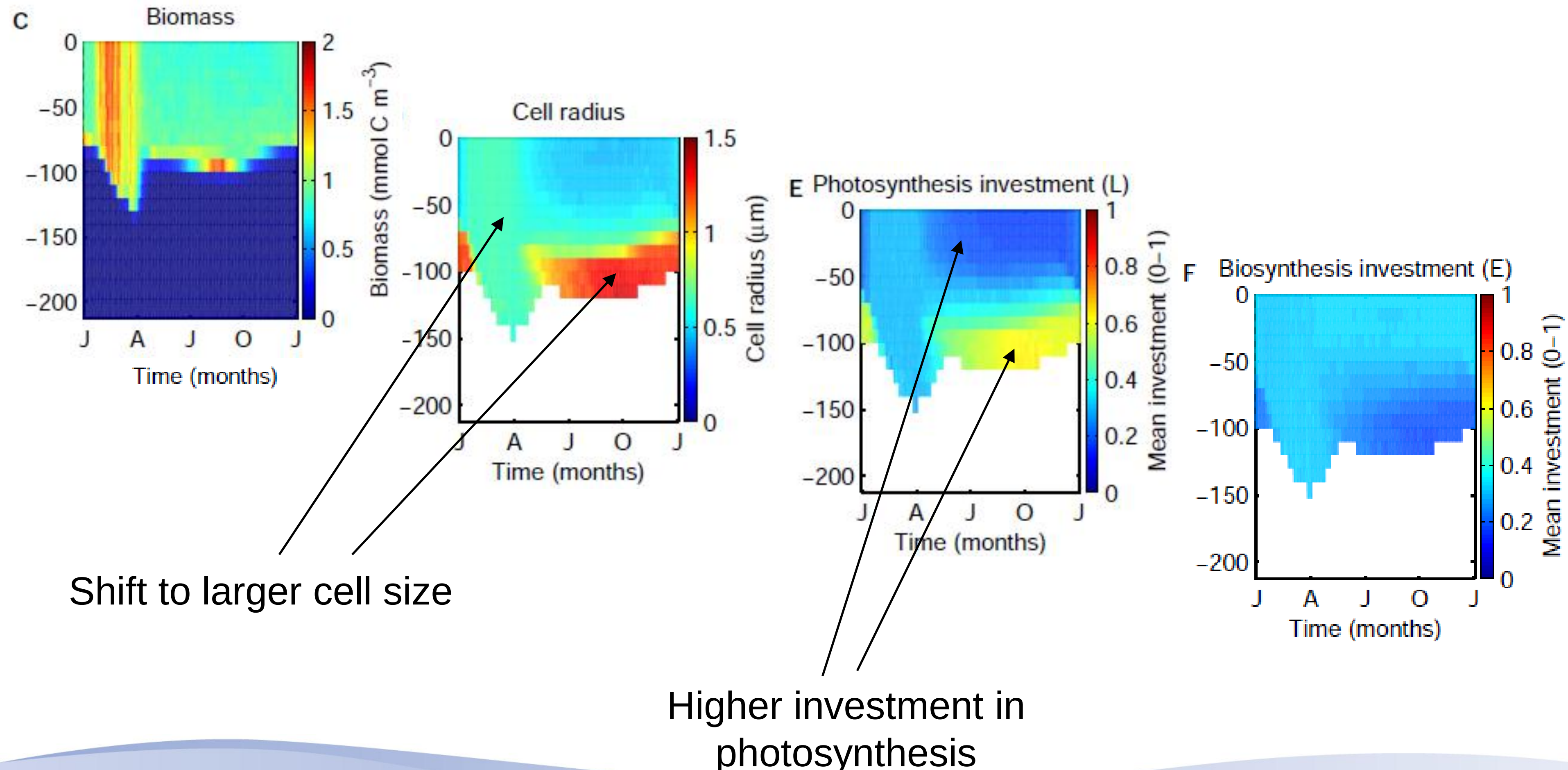
- Shift to larger cell sizes (~0.7µm) in *Prochlorococcus* during the spring bloom.
- Larger cell sizes generally observed at depth, around the deep chlorophyll maximum.

- High light adapted species dominate in well mixed surface waters.
- In stratified conditions, shift to low light adapted species at depth.



Malmstrom (2010)

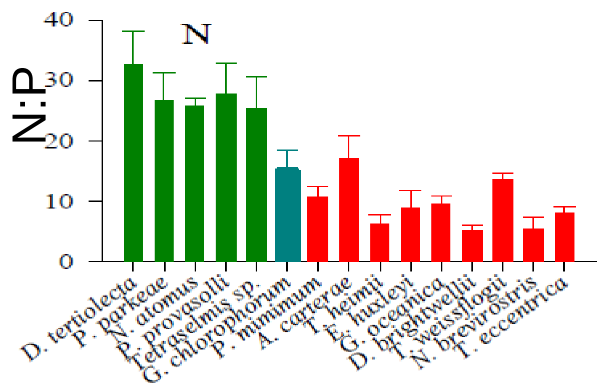
Phytoplankton population dynamics at BATS



Clark, Lenton, Williams, Daines (2013) *Limnol. Oceanog.* 58: 1008-1022

2. Patterns in phytoplankton N:P stoichiometry

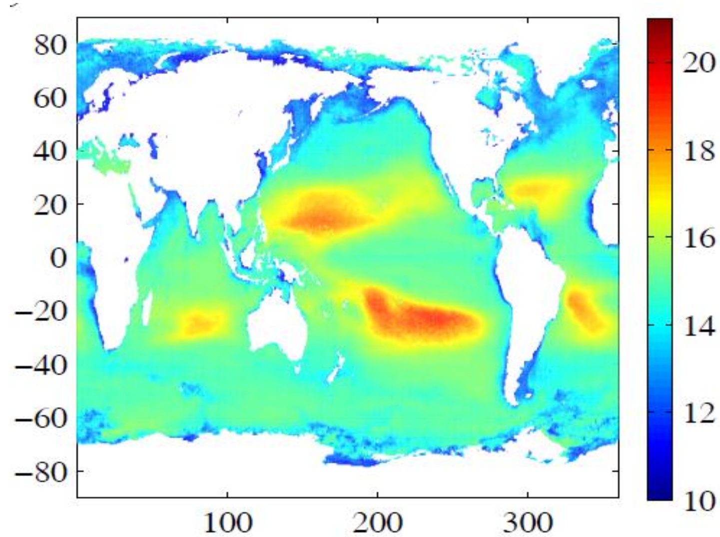
Phytoplankton stoichiometry in laboratory culture
Quigg etal (2003) Nature



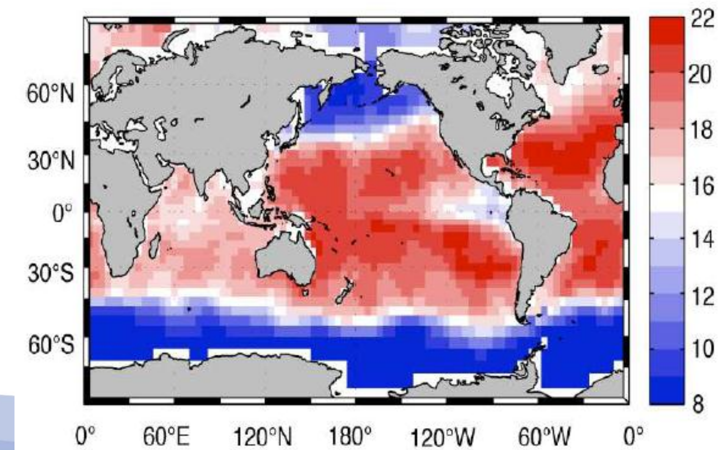
'Greens'
Ostreococcus

Prokaryotes:
Prochl.
Synecoccocus

'Reds'
Diatoms
Cocolithophores



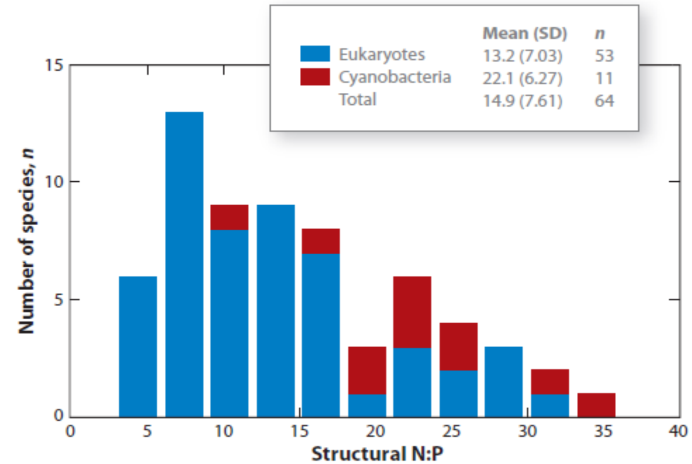
N:P from chl and size-class weighting (Daines et al. 2013)

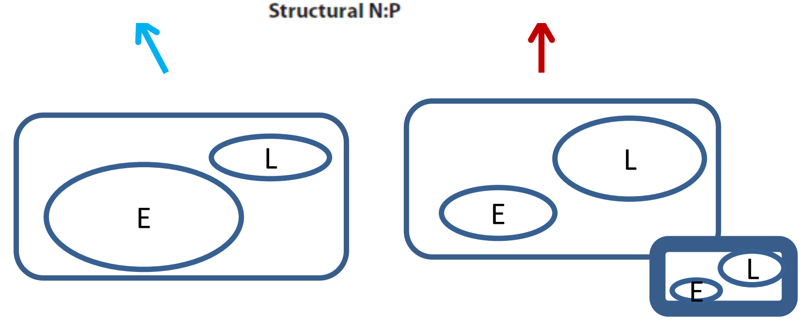


N:P from diatom (Si export) weighting (Weber & Deutsch 2012)

The growth rate hypothesis, rRNA and N:P

- Maintaining high growth rates requires high concentrations of P-rich ribosomes (rRNA)
- Predict that faster growth rate produces lower N:P organisms
- Crucial to determining how low N:P can go is the rRNA ‘rate constant’ for protein synthesis (aa rib^{-1} s^{-1})



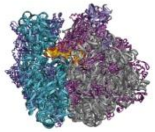


Fast growth
P rich ribosomes
Low N:P

Resource limited
Slow growth
High N:P

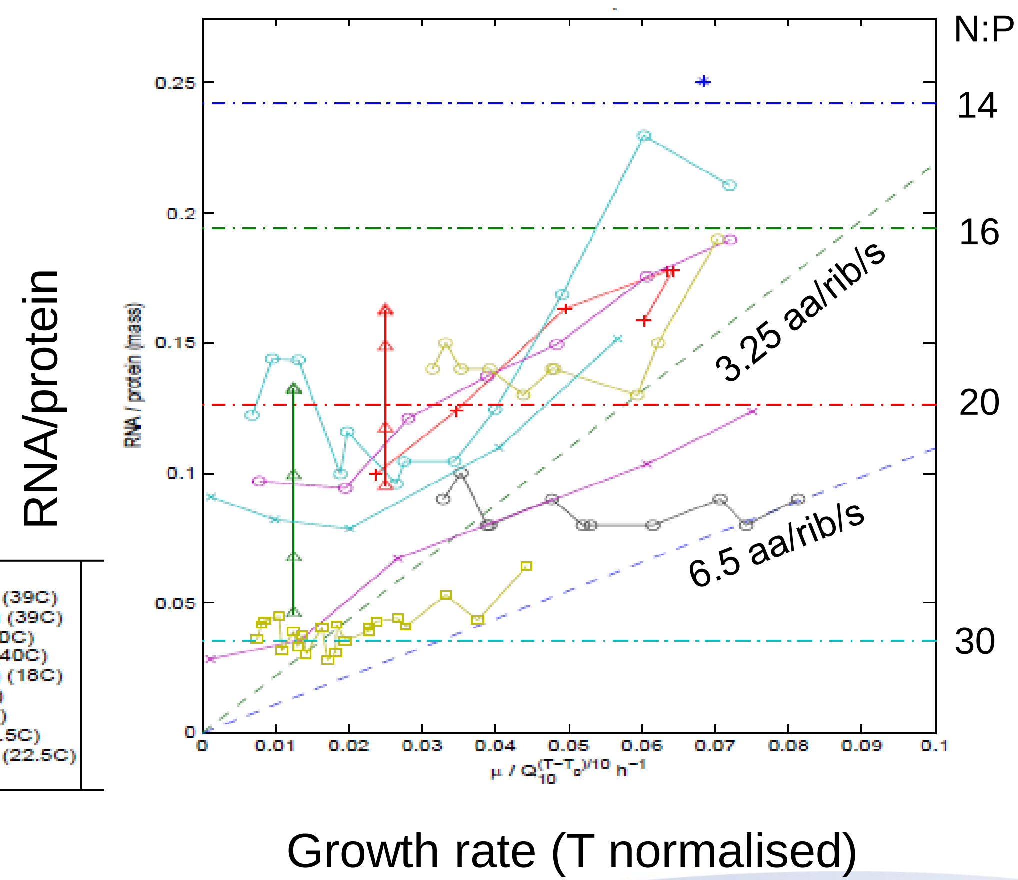
Klausmeier *et al.* (2004) *Nature* 429: 171-174

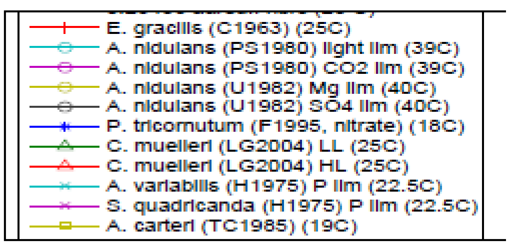
Deutsch & Weber (2012) *Ann. Rev. Mar. Sci.* 4: 113-141



rRNA required for protein synthesis

- Existing models span a range 2.7–5.7 aa rib^{-1} s^{-1}
- High value is from yeast (heterotrophic fungus!)
- New compilation of data for photoautotrophs





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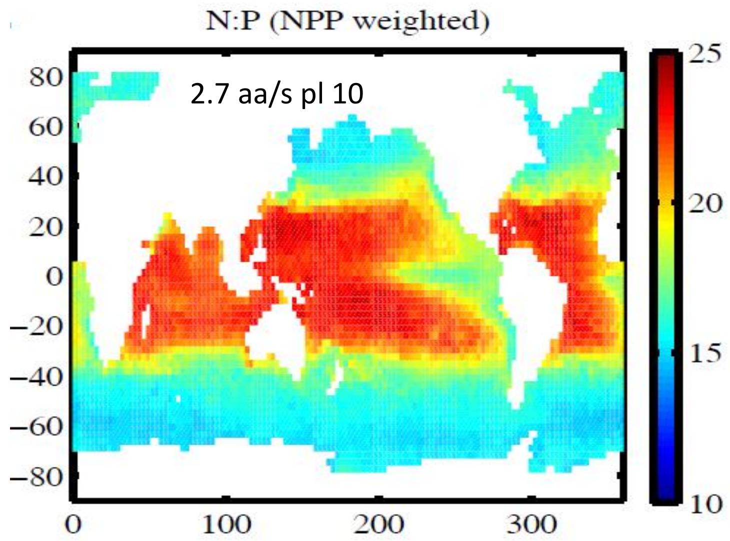
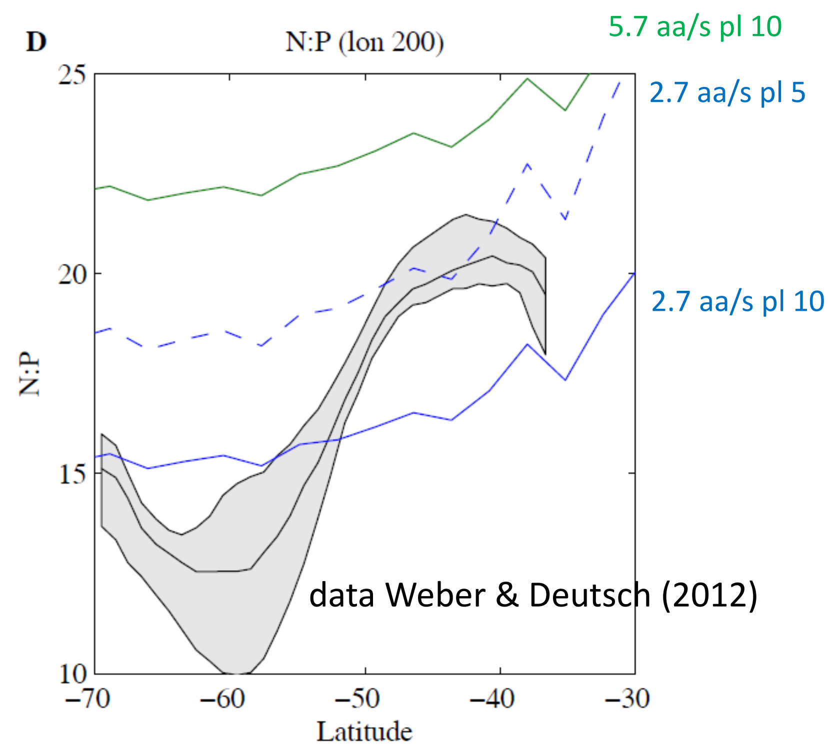
Daines, Clark, Lenton (2013) *Ecol. Lett.* in review

Predictions from the growth rate hypothesis





- Explains overall patterns in N:P
- But not lowest observed N:P
- Additional contribution from P storage?

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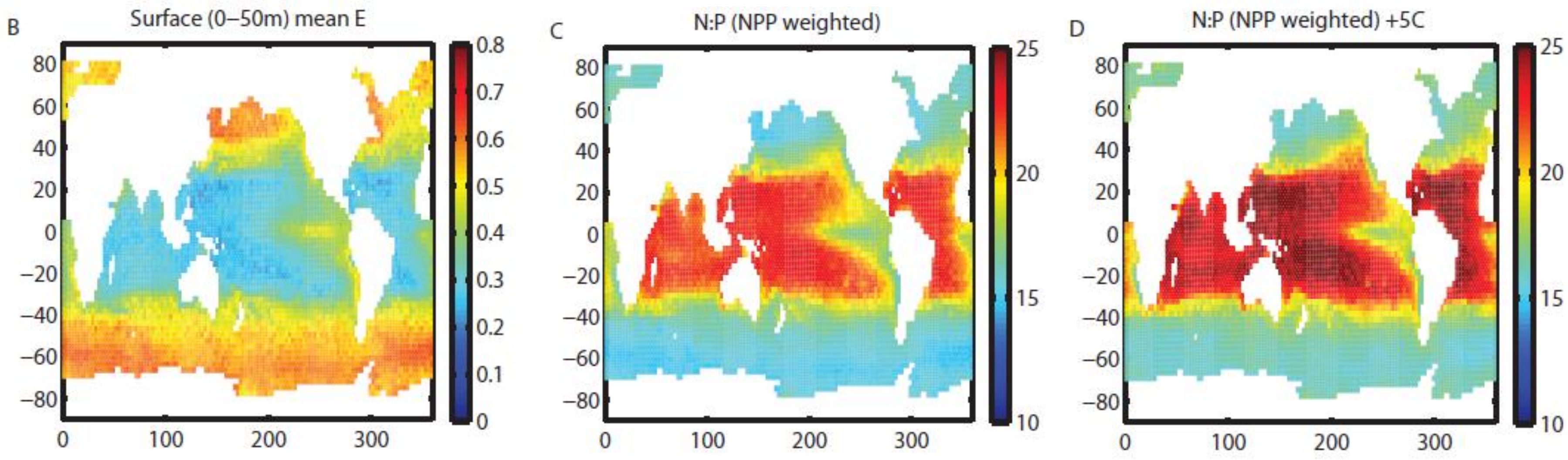
Daines, Clark, Lenton (2013) *Ecol. Lett.* in review

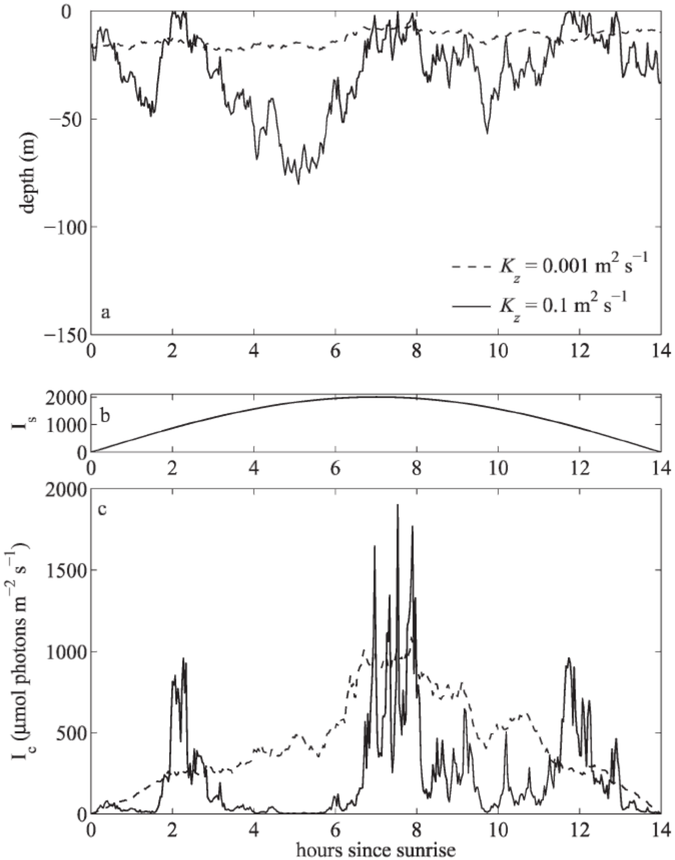
Physiological effect of warming



- Rate of protein synthesis increases strongly with temperature
- Less P-rich ribosomes required to produce required N-rich protein at higher T
- Therefore physiological effect of warming is to increase organism N:P
- But must also consider effects of increased stratification reducing nutrient supply...

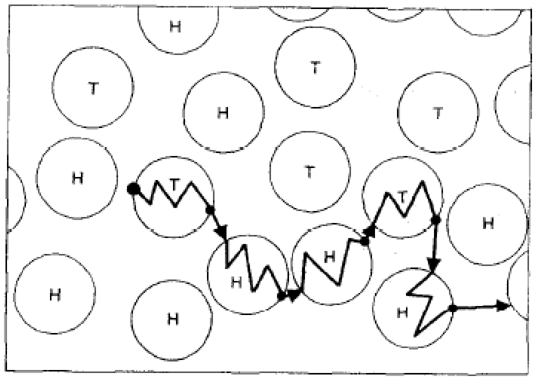
Toseland, Daines, Clark, *et al.* (2013) *Nature Climate Change* in press

3. Strategies for dynamic environments



e.g. Fluctuating light environment in mixed layer (Ross *et al.* 2008)

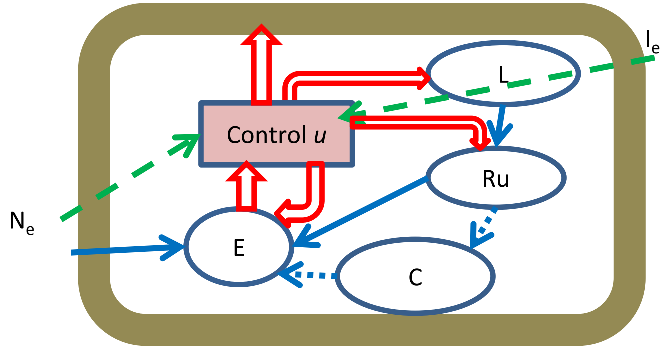
- Autotroph storage pools even out stochastic supply of light, N, P
- But how to model this?...

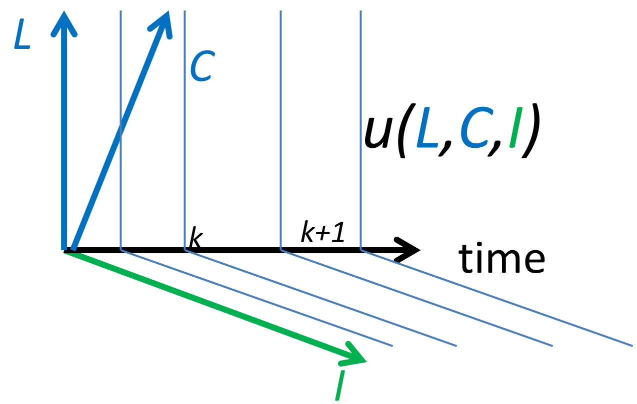


Optimal foraging – MacArthur & Pianka (1966), Emlen (1966), Charnov (1976)...

Storage and acclimation as optimal control

- Fitness benefit of dynamic allocation (acclimation, storage)

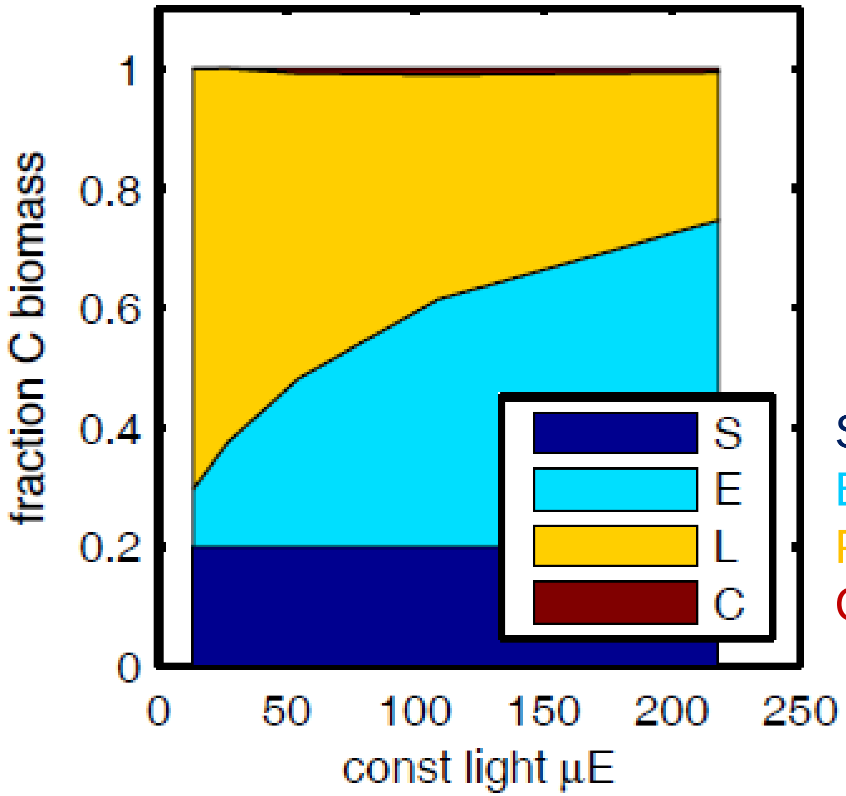




$$\underbrace{J_k^*(x_k, e_k)}_{\text{Fitness (eg biomass)}} = \max_{u_k} \overbrace{\mathrm{E}}^{\text{Expectation over stochastic environment}}_{w_k} \Big\{ \underbrace{g_k(x_k, e_k, \overbrace{u_k(x_k, e_k)}^{\text{control}}, w_k)}_{\text{Instantaneous benefit}} + \underbrace{J_{k+1}^*(\overbrace{F_k(x_k, e_k, u_k, w_k)}^{\text{state evolution (growth!)}})}_{\text{Future benefit}} \Big\}$$

Daines (2013) *Am. Nat.* in revision

One optimal strategy in constant environment – no C storage



Structure
Biosynthesis
Photosynthesis
Carbon storage

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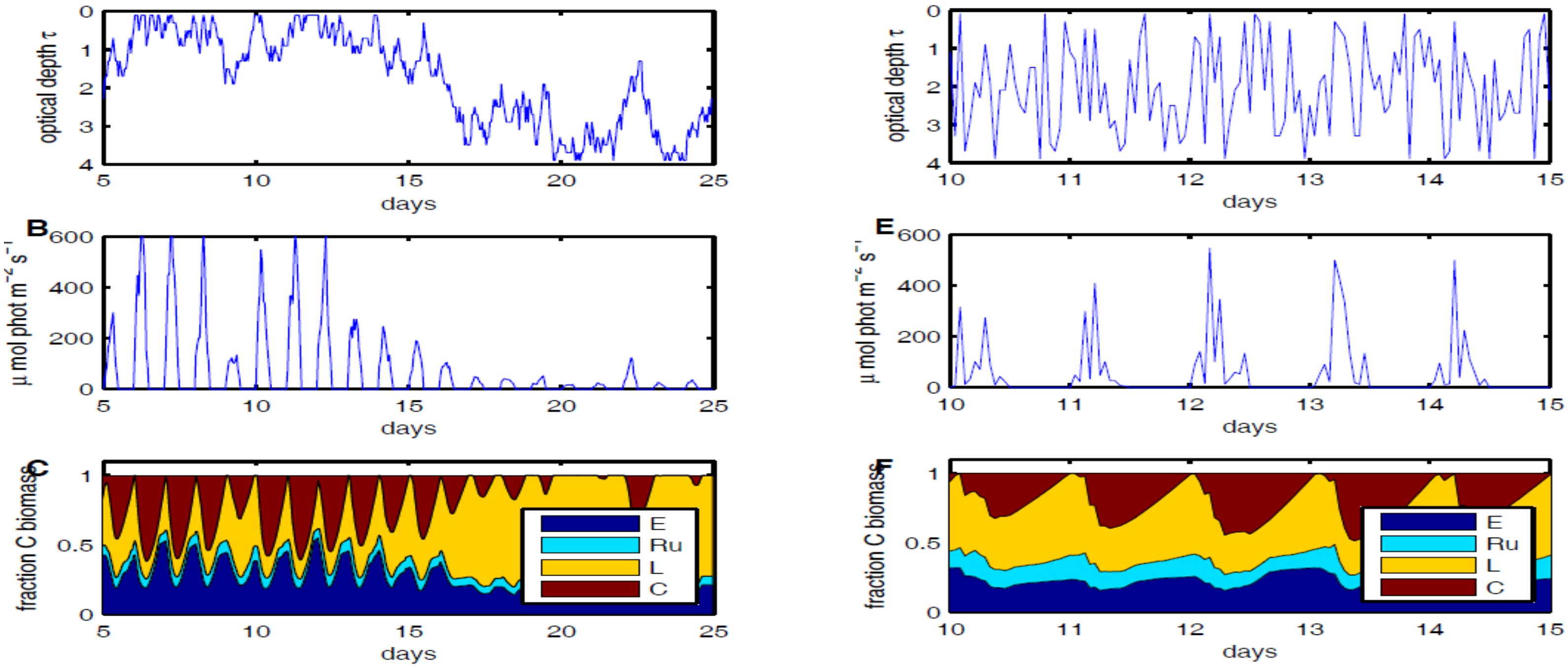
Daines (2013) *Am. Nat.* in revision

Emergent strateg*ies* in fluctuating environments

Slow variability – C storage over diel cycle, acclimation

cf Ross & Geider (2009)

Fast variability – fitness maximisation
⇨ increased allocation to Rubisco, C storage buffering of short light pulses



Structure
Biosynthesis
Photosynthesis
Carbon storage

Daines (2013) *Am. Nat.* in revision

Summary

- Approach of physiology + resource allocation + optimality gives a parameter-sparse representation of diversity:
  - Environmental selection on *traits (population adaptation)*
  - Dynamic environments: fitness maximising behaviour as *optimal control (acclimation, storage strategies)*
- Environmental selection for phytoplankton growth strategies
  - Size: Nutrients ⇨ (minimum) size
  - Composition: overall patterns in N:P
  - ... but growth rate requirements for rRNA can only explain part of N:P
  - Dynamic strategies as fitness maximisation
- Functional trait and physiological approach is *unreasonably* effective …as an approach to evolutionary ecology

Implications for the carbon cycle

- C:N is relatively conserved therefore predicted increase in N:P under warming implies increased C:P and potentially greater export
  - But need to consider changes in multiple environmental controls
- Increase in phytoplankton N:P will tend to produce more N limitation, but may also select more strongly for diazotrophs
- Need dynamic strategies to capture storage of C, P and N in phytoplankton properly

Integrative Terrestrial-Marine Lessons

- Traits and physiologically-grounded trade-offs is the way forward for process-based prediction (cf Tilman 1990, JeDi terrestrial model)
- Marine: Primary production by microbes in fluid
  - Relatively direct link from cellular economics and ecophysiology to biogeochemical cycles (but recycling still ‘complicated’ and higher organisms and trophic structure important for biological pump)
  - High diversity and rapid adaptation of microbial ecosystem
  - Fluid physical environment ‘easy’ to model
- Terrestrial: Primary production by higher plants in soil
  - Multi-cellular complexity and soil formation means indirect link from ecophysiology and cellular economics to biogeochemical cycles
  - Long lifetimes, slow dispersal, slower adaptation timescales
  - Solid phase of physical environment ‘hard’ to model

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